Biofacies Analysis of Upper Cretaceous Deposits in the Ust-Yenisei Region: Implications of Palynomorphs

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Abstract—The results of palynomorph biofacies analysis in the Upper Cretaceous deposits of the Ust-Yenisei region are presented. The established facies confinement and indicative features of separate palynomorph groups are used, along with identified dinocyst morphotypes and taxa, in paleogeographic reconstructions. Seven palynomorph assemblages characterizing continental, coastal-marine, shallow- and deep-water facies are distinguished based on quantitative proportions between morphological groupings and individual taxa. As boundaries between distinguishable biostratigraphic and facies subdivisions do not coincide, dinocysts were likely insignificantly dependent in distribution on facies in the West Siberian epicontinental basin at least. On the other hand, distribution trends of particular dinocyst morphotypes and other microphytofossils are correlative with transgressive-regressive cycles and can be used for reconstruction of paleoenvironments.

INTRODUCTION

When solving problems of facies, paleogeographic and paleolandscape reconstructions, an actual objective is to study jointly the different palynomorph groups (spores and pollen of terrestrial plants, dinoflagellate cysts, prasinophytes, acritarchs, zygnematacean algae, and taxa of unclear taxonomic affinity) in different sedimentary facies, their ecologic characteristics, and principal trends of distribution under influence of abiotic factors. Being buried in sediments of variable continental and marine genesis, spores and pollen of terrestrial plants can be indicative, along with the other data, of the shoreline position in the past, provenance localization, directions of paleocurrents, etc. Among unicellular algae, there are forms characterizing a broad spectrum of habitats from freshwater basins to deep-water marine settings. Seeking for dependence of microphytoplankton on different environmental factors, it is necessary to consider basic information of different kind: first, data on ecology of present-day taxa and, second, proportions of palynomorphs in palynological assemblages, dynamics of their diversification, prevalence and relative abundance of separate genera and species in well-studied sections, where facies subdivisions are confidently defined based on sedimentological, paleontological and geochemical data. Interpreting the fossil assemblages, we should pay attention to all microphytofossils macerated from rock samples for palynological analysis. In addition to spores and pollen of terrestrial plants and dinocysts, the assemblages commonly include prasinophytes (phylum Chlorophyta, class Prasinophyceae), spores of zygnematacean algae (phylum Chlorophyta, class Zygnemataceae), and acritarchs (a group of unclear taxonomic affinity).

This work is an attempt to establish how distribution of some palynomorph taxa, composition and structure of palynological assemblages depend on particular environments reconstructed based on lithological and paleontological data obtained in a section of Upper Cretaceous deposits in the Ust-Yenisei region. This section of the Cenomanian–Maastrichtian deposits is composed of interlayering continental and marine deposits, the latter being dominant (Fig. 1). The section was deposited in a shallow northeastern bay of the West Siberian epicontinental basin. It is of the reference type being very complete, studied well and composed of variable facies containing abundant macrofauna and diverse assemblages of microphytofossils.

MATERIAL AND INVESTIGATION METHODS

The samples studied have been collected during my fieldworks in the Ust-Yenisei region (the Upper Cretaceous sections exposed along the Nizhnyaya Agapa, Chaika, Yangoda, and Tanama rivers and near the settlement Vorontsovo). A high-resolution sampling and diversity of microphytofossils in nearly all the sections provided an opportunity to analyze distribution of different palynomorph groups depending on facies. The dependence is established using diagrams, which illustrate the taxonomic composition and diversity of assemblages, visualizing the quantitative proportions of separate genera, species or morphological groupings among the microscopic marine algae, the species diver-
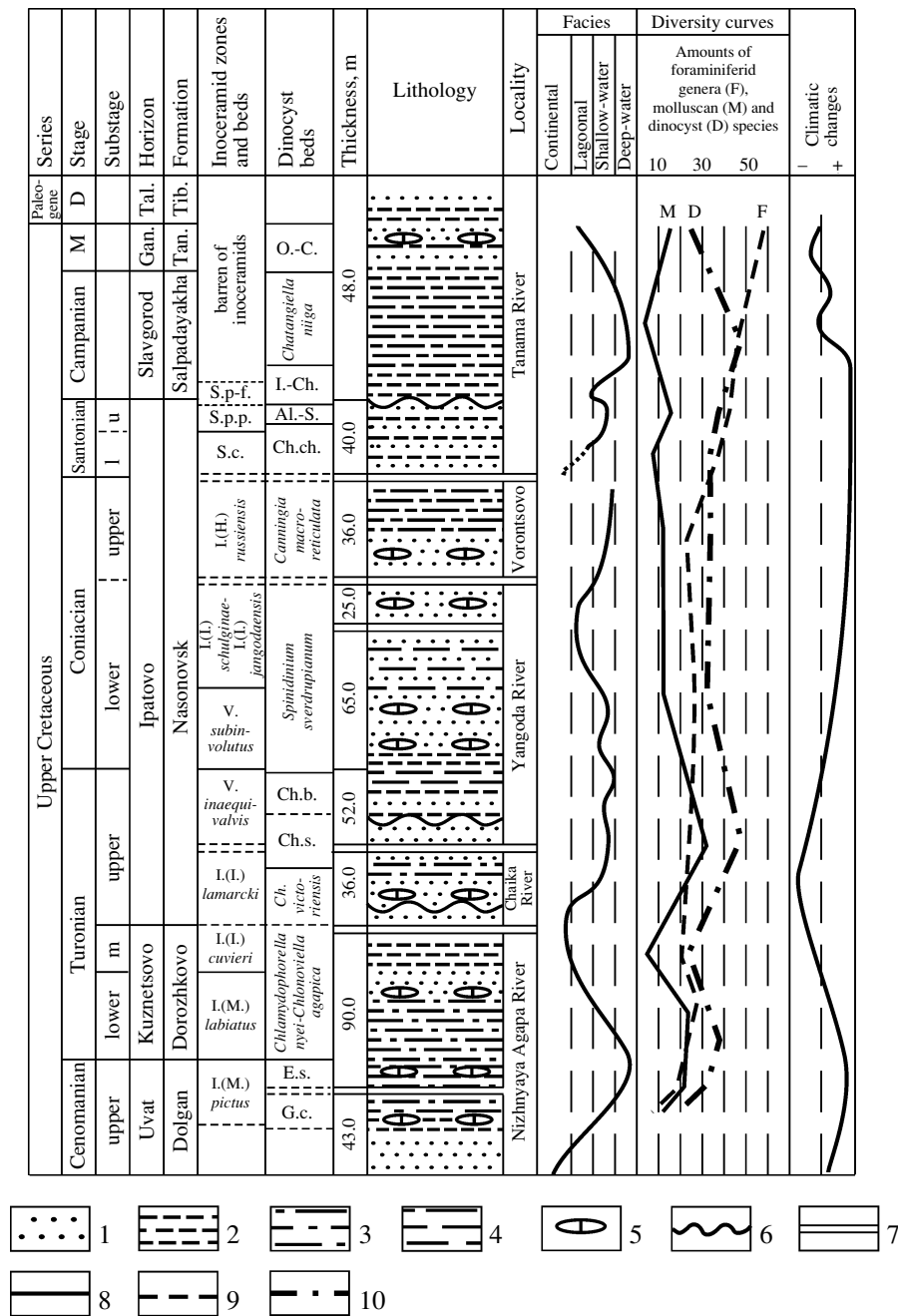
Fig. 1. Integrated Upper Cretaceous succession of the Ust-Yenisei region and main biotic and abiotic events (after Zakharov et al., 2003): (1) sand; (2) aleurite; (3) silty clay; (4) clay; (5) calcareous concretions; (6) break in sedimentation; (7) break in observations; (8–10) curves characterizing diversity of benthic mollusks (8), foraminiferid genera (9) and dinocyst species (10). Stages and substages: (M) Maastrichtian, (D) Danian, (l) lower, (m) middle, (u) upper. Horizons and formations: (Gan.) Gan'kino, (Tal.) Talitsa, (Tan.) Tanama, (Tib.) Tibes. Inoceramid zones and beds: (I) *Inoceramus*, (M) *Mytiloides*, (V) *Volviceramus*, (H) *Haenleinia*, (S) *phenoceramus*, (c) *cardissoides*, (p) *patootensis*, (p-f) *patootensiformis*. Dinocyst beds: (G. c.) *Geiselodinium cenomanicum*; (E. s.) *Eurydinium saxoniense*; (Ch. s.) *Chatangiella spectabilis–Oligosphaeridium pulcherrimum*; (Ch. b.) *Chatangiella bondarenkoi–Pierceites pentagonum*; (Ch. ch.) *Chatangiella chetiensis*; (Al.-S.) *Alterbidinium* spp.–*Spinidinium echinoideum*; (I.-Ch.) *Isabelidinium* spp.–*Chatangiella verrucose*; (O.-C.) *Operculodinium centrocarpum–Cerodinium diebelii*.

sity of dinocysts, and percentages of prasinophytes, acritarchs, microforaminifers and zygnematacean algae. The proportion between terrestrial (spores, pollen, freshwater algae) and marine components (dinocysts, prasinophytes, acritarchs) is estimated relative to sum of all the palynomorphs taken for 100%. Percentages of different groups in composition of microphytoplankton are calculated relative to sum of dinocyst, acritarch and prasinophyte specimens only.

When seeking for facies dependence, I considered not only individual taxa but also groups of genera having similar morphological structures. Basic genera representing each of the groups are listed below. The Spiniferites and Cyclonephelium are individualized as suggested by Li and Habib (1996). Spiniferites: *Spiniferites, Achomosphaera, Oligosphaeridium, Hystrichosphaeridium, Hystrichodinium, Avelodinium.* Cyclonephelium: *Cyclonephelium, Exochosphaeridium, Cleistosphaeridium, Kiokansium, Micrhystridium, Sentusidinium.*

Cavate cysts: *Eurydinium, Trithyrodinium, Palaeohystrichophora, Alterbidinium, Odontochitina, Deflandrea, Subtilisphaera, Spinidinium, Isabelidinium, Chatangiella.*

Proximate and proximochorate cysts: *Gonyaulacysta, Rhyptocorys, Microdinium, Eisenackia, Glyphanodinium, Trichodinium, Cribroperidinium, Apteodinium, Kallosphaeridium, Canningia, Cyclonephelium, Circulodinium, Laciniadinium, Dorocysta* and others.

Chorate cysts: representatives of the *Spiniferites* coupled with *Surculosphaeridium, Heterosphaeridium, Exochosphaeridium, Coronifera, Pterodinium, Florentinia, Cleistosphaeridium, Pervosphaeridium, Raetiaedinium, Membranilarnacia* and others.

Holocavate cysts: *Chlonoviella, Chlamydophorella, Membranisphaera.*

Pterospermella group: *Pterospermella, Cymatiosphaera.*

Paralecaniella group: *Paralecaniella, Leiosphaeridia.*

Schizosporis group: *Schizosporis, Shizocysta, Hydropteris.*

BRIEF INFORMATION ON ECOLOGY OF DINOFLAGELLATES, THEIR CYSTS AND OTHER PALYNOMORPHS

Present-day dinoflagellates are very diverse in ecologic aspect. They inhabit marine, brackish and fresh waters. According to Taylor (1987), 90% of recent dinoflagellates dwell in seas and only 10% in fresh waters. Let us consider some most important factors influencing distribution of recent dinoflagellates.

Temperature is a basic characteristic of water that controls the latitudinal distribution of dinoflagellates. Tolerance of dinoflagellate species, which can dwell within a broad range of temperature from –27 to +38°C, is variable (Taylor, 1987). In majority, dinoflagellate habitats are constrained by particular latitudinal zones. Eurythermal dinoflagellate species are usually cosmopolitan, whereas stenothermal taxa dwell in warm waters as a rule. Temperature controls viscosity and density of water. The viscosity factor is likely responsible for relative prevalence of dinoflagellates in tropical basins and diatoms in subpolar regions. On the other hand, the vertical migration of organisms from surface waters depleted in nutrients into deeper water layers enriched in nourishing components is of a great importance. Dinoflagellates, the active swimmers, can occupy an optimal position in the water column.

Morphology of dinoflagellate theca depends on the habitat environments. As is established, thecae of tropical species, as compared to those of cold-water forms, have thinner walls but longer horns and processes. Enlargement of the cell surface area under conditions of lower viscosity is especially important for cyst-forming species. For instance, gonyaulacoid forms producing largely the chorate cysts are common habitants of tropical and temperate neritic settings. Peridinioid species forming in general the proximate cysts are typical most frequently of cold waters, although some of them occur in moderately warm waters as well.

Biogenic elements. For their normal life activity, algae need in macro- (carbon, hydrogen, oxygen, phosphorus, nitrogen) and microelements (magnesium, iron, copper, manganese, zinc, molybdenum, sulfur, potassium and calcium). As a rule, waters are commonly rich enough in oxygen and carbon dioxide, the biophile elements most important for life activity. Elements, which constrain the algae growth and productivity, are nitrogen in marine settings and phosphorus in freshwater basins. As the euphotic zone becomes depleted in nitrogen, when phytoplankton sinks in deeper waters, hydrodynamics and convection currents play an important role (Zonneveld et al., 2001). Influx of nutrients in upwelling zones leads to the productivity growth. Dinoflagellates consume nutrients through the cell surface, and the surface-to-volume ratio of cell (S/V) is therefore growing when biogenic elements are in deficiency (Harrison et al., 1977), i.e., small algae with high S/V ratio get privilege in oligotrophic (depleted in nutrients) waters.

Salinity. Dinoflagellates existing at present are confined mostly to sea basins with salinity of 20–30‰ or more. Freshwater species do not survive salinity over 5‰. Being variably adaptable and tolerant to salinity variations, dinoflagellates are divisible into eury- and stenohaline taxa (Taylor, 1987). The euryhaline dinoflagellates populate the estuarine niches only. Influence of salinity on dinoflagellates is studied insufficiently well, and distribution of dinoflagellates in neritic, brackish-water and freshwater settings is outlined in a very schematic mode only. Hulburt (1963) who studied phytoplankton of the Northwest Atlantic established that populations of open ocean are small, being larger on continental shelf and the largest in estuaries. In the last settings there is observable decrease of species diversity and sometimes prevalence of one species in community.

Study of dinoflagellates in the Masan Bay, South Korea (Yoo, 1991), and experiments in marine ecosystems (Hinga, 1992) showed a distinct positive correlation between abundance of dinoflagellates and pH of waters. As is assumed, pH is one of important factors controlling bloom of dinoflagellates in coastal zone.

Fossil dinoflagellates are represented by their cysts composed of resistant sporopollenin. The process of cyst formation is known inadequately that is a serious obstacle for paleofacies and paleoecological reconstructions, as we face the problem to compare two types of assemblages. The planktonic vegetative stage of dinoflagellates is a part of biocoenosis, whereas their cysts accumulated in sediment represent a "projection onto bottom" of ecologically diverse planktonic communities, which existed in the stratified water column.

Book by Wall et al. (1977), where authors have analyzed 168 assemblages in samples collected from estuaries, continental shelves and slopes, and from abyssal plains, is a largest summarizing work dedicated to distribution of recent dinocysts. Authors who considered data on dinocysts from 14 geographic regions of the North and South Atlantic, Caribbean and Mediterranean seas, and the Southeast Pacific formulated two following presumptions. (1) The main factor controlling distribution of dinocysts in sediments is relationship between species and types of waters divided into the estuarine, coastal, transitional coastal–oceanic and oceanic. Despite the cosmopolitan character of most species, there is a tendency of their confinement to definite bathymetric zones. (2) Distribution of dinocysts is also under control of latitudinal factor and climatic fluctuations, and the latitudinal differentiation is most obvious in coastal zones. There was also a series of publications considering distribution of recent and Quaternary dinocysts as dependent on their habitat environments, and many of these comprehensive works are certainly valuable (Goodman, 1987; Sarjeant et al., 1987; Harland, 1988; Mudie and Harland, 1996; Dale, 1996; Marret and Zonneveld, 2003; and others).

Nevertheless, ecological interpretation or recent dinocysts is not always applicable to fossil materials. First, fossil genera and species are extinct, and second, their ecological adaptation to habitat environments could be changing with time. Considered below are some, though not all the ecological aspects of fossil dinocysts, because they are used in this work.

Morphology and Taxonomy

There is a viewpoint that proximate cysts with short thick serrate processes are indicative of coastal brackish-water environments, whereas chorate cysts with long complicated processes suggest environments of open sea (Vozzhennikova, 1965; Williams, 1975; Tappan, 1980; Sarjeant et al., 1987; and others). According to other works, species of comparable morphology may occur in very different settings. Besides, Wheeler and Sarjeant (1990) regard the morphological approach as more important for obtaining the paleoecological information than the taxonomic one.

Data on confinement of particular dinocyst taxa to certain environments are often controversial. For instance, their assemblages dominated by the chorate *Spiniferites* forms with long processes have been regarded as indicators of open sea environments (Downie et al., 1971; Davey and Rogers, 1975; Brinkhuis and Zachariasse, 1988; Marshall and Batten, 1988; Eshet et al., 1994). At the same time, the genus *Spiniferites* has been considered as typical representative of dinocysts characteristic of the outer and inner shelf (Wrenn and Kokinos, 1986; Head and Wrenn, 1992). In recent sediments however, the maximum abundance of *Spiniferites/Areoligera* group is established in estuaries and innermost shelf zone (Wall et al., 1977). In addition, Hultberg and Malmgren (1986) who studied the Maastrichtian dinoflagellates in Denmark and Sweden showed that the increasing abundance of *Spiniferites* forms and general decrease of dinocysts' diversity are correlative with regression and shoaling in the basin.

Assemblages with cysts similar to *Cyclonephelium* are thought to be characterizing the coastal settings (Liengjarern et al., 1980; Brinkhuis and Zachariasse, 1988; Marshall and Batten, 1988; Eshet et al., 1994). On the other hand, Harris and Tocher (2003) who studied diverse facies of the Cenomanian–Turonian deposits in the Western Interior Basin, the United States, demonstrated that this genus includes species having different facies affinity. Par example, *Circulodinium brevispinatum* (Mill.) Fauc. and *Cyclonephelium vannophorum* Dav. are typical of low-salinity environments, whereas *Cauveridinium membraniphorum* (Cook. et Eis.) Mas. and *C. compactum* Defl. et Cook. are characteristic of settings most remote from coastline. Similarly, *Oligosphaeridium pulcherrimum* (Defl. et Cook.) Dav. et Will. and *O. totum* Brid. are connected with environments of lowered and normal salinity, respectively. In addition, Harris and Tocher (2003) noted a much higher content of chorate forms with long processes (*Dapsilidinium, Hystrichodinium pulchrum, ?Surculosphaeridium longifurcatum* (Firt.) Dav. et al.) in deep-water parts of the basin and simultaneously discovered many chorate cysts (*Coronifera oceanica* Cook. et Eis., *Exochosphaeridium phragmites* Dav. et al., *Florentinia, Hystrichosphaeridium*, and *Oligosphaeridium* forms) in its marginal parts.

Assemblages with dominant peridinioid cysts of the *Wetzeliella* type presumably suggest lagoonal or brackish-water settings (Downie et al., 1971; Davey, 1971; Wall et al., 1977; Bujak, 1984). Representatives of the genus *Chatangiella* studied in a section of the Santonian–Campanian coastal-marine deposits of the Ust-Yenisei region are predominantly confined to sandy siltstones and fine-grained sands (Khlonova and Lebedeva, 1988; Lebedeva, 2001). Besides, May (1980) established an abundance peak of *Chatangiella tripartite* (Cook. et Eis.) Lent. et Will. in deposits of inner and outer shelf. Assemblages of peridinioid (diverse *Chatangiella* forms inclusive) and chorate dinocysts characterizing marine settings with different salinity are known from the Interior Plains of North American continent (Harker et al., 1990).

May (1980) who studied microphytoplankton of low diversity from the Upper Cretaceous deposits of New Jersey suggested that prevalence of *Dinogymnium* in assemblages is indicative of estuarine environments. Channels in walls and corrugated structure of some *Dinogymnium* forms could prevent hurting of cells, when they changed volume under extreme salinity fluctuations in estuarine environments.

Anoxic Environments

Numerous data obtained recently characterize behavior of dinocysts and other representatives of microphytoplankton during the anoxic events (in the so-called "stagnation levels"). The problem is considered in some publications (Lebedeva and Zverev, 2003; Lebedeva, 2002).

Salinity

Despite many works dedicated to consideration of coastal–deep-water and neritic–oceanic assemblages of microphytoplankton, the salinity influence on respective organisms is poorly understood. Multidisciplinary (lithological, geochemical, paleontological) study of the upper Cenomanian–lower Turonian deposits have been performed with a high stratigraphic resolution in the West Interior basin of North America along a sedimentary profile characterizing a succession of sedimentation settings from proximal coastal with lowered salinity to deep-water and coastal-marine with normal salinity (Harris and Tocher, 2003). As is concluded in the cited work, the salinity factor is of a greater influence on distribution of dinocysts than the basin depth or distance from coastline. Harris and Tocher distinguished three groups of the species studied: (1) euryhaline *Canningia reticulate* Cook. et Eis., *Circulodinium colliveri* (Cook. et Eis.) Helby, *C. brevispinatum, Coronifera oceanica, Cribroperidinium cooksoniae* Norv., *Cyclonephelium vannophorum, Oligosphaeridium pulcherrimum*, and others, which were tolerant to or presumably preferred the lowered salinity; (2) stenohaline *Apteodinium deflandrei* (Clarke et Verd.) Luc.-Clark, *Eurydinium eyrensis* (Cook. et Eis.) Stov. et Evitt, *Leberidocysta deflocata* (Dav. et Verd.) Stov. et Evitt, *Subtilisphaera pirnaensis* (Alb.) Jain et Mill. and others, which preferred the normal salinity; (3) *Adnatosphaeridium tutulosum* (Cook. et Eis.) Morg., *Chlamydophorella discreta* Clarke et Verd., *C. nyei* Cook. et Eis., *Dapsilidinium laminaspinosum* (Dav. et Will.) Lent. et Will., *Ellipsodinium rugulosum* Clarke et Verd., *Isabelidinium magnum* (Dav.) Stov. et Evitt, *Pterodinium cingulatum* (Wetz.) Bel., *P. ?cornutum* Cook. et Eis., *Rhiptocorys veligera* (Defl.) Lej.-Carp. et Sarj. and others, which dwelt away from coastline. Many of these species turned out to be widespread in a wide spectrum of environments. As is established (Harris and Tocher, 2003), peridinioid cysts dominate in settings with a low salinity and high content of terrestrial components.

Remoteness from Coastline, Transgressive-Regressive Events, etc.

In many works, researchers tended to determine groupings of dinoflagellates characterizing remoteness of their habitat zone from the coastline, and in some works, successive assemblages of phytoplankton have been interpreted as connected with respective transgressive-regressive phases. Prauss (1989) established a succession of microphytoplankton assemblages interrelated with transgressive-regressive trend in evolution of the Toarcian–Aalenian basin in northwestern Germany, where the dinocysts – acritarchs – prasinophytes cycle corresponded to the regressive phase and the reversed cycle to the transgressive one. This model is consistent with data of V.A. Fedorova (Shakhmundes, 1973) on the Lower Cretaceous deposits in the North Caspian region.

The species diversity is parameter extensively applicable in paleoecology of dinocysts. In general, this parameter changes away from coastline: assemblages of distal shelf are more diverse than in proximal shelf zone (Wall et al., 1977; Dale, 1983). Just as the other organisms, dinoflagellate species grow in number during enlargement of their habitat area. Consequently, widening of continental shelf during sea transgression provides new habitats and leads to species diversification (MacArthur and Wilson, 1967). Dependence of the dinocyst species diversity on three cycles of relative sea-level fluctuations has been considered in work by Habib et al. (1992).

Some researchers are of opinion that an eustatic sea-level rise leads to a fast increase of dinoflagellate species amount, and a comparable "dinoflagellate invasion" can be used to interpret an event of this kind (Partridge, 1976). Wall et al. (1977) showed that the species diversity index of present-day cysts grows away from coast of the Atlantic Ocean. As noted by May (1980), a comparatively low diversity of current species, one or two of which are dominants, is a characteristic feature of assemblages from coastal (estuarine) sediments. Habib and Miller (1989) considered the increasing species diversity of dinoflagellates as indicative of marine transgression.

Harland (1973) proposed to determine a qualitative extent of remoteness from shore by means of special index corresponding to ratio between amounts of gonyaulacoid and peridinioid dinocysts species: the higher ratio implies the longer offshore distance. Interpretation of this parameter is ambiguous however, because peridinioid cysts are very different in their ecologic preferences, as is shown above. According to Dale (1976), recent microphytoplankton assemblages from fjords of Norway are dominated by acritarchs, and gonyaulacoid cysts prevail in them over peridinioid ones

despite a great abundance of peridinioid thecae in the living planktonic community. It has been noted also that the above index ignores the amount of individual cysts, being based on the amount of species only, some of which represented by single specimens can be allochthonous, i.e., transported by currents to the site of burial from outside (Harker et al., 1990). Hence, in opinion of the cited authors it would be incorrect to rely on that index only when determining the transgressive-regressive phases of sedimentation.

Analyzing distribution of dinocysts in the Campanian–Maastrichtian sediments deposited in different settings of coastal zone and external shelf, May (1980) distinguished four types of their assemblages. (1) The *Dinogymnium pustulicostatum* assemblage: significantly abundant *D. pustulicostatum* May, *Spinidinium ornatum* (May) Lent. et Will., *Palaeohystrichophora infusorioides* Defl., and *Trithyrodinium robustum* Ben.; insignificant species diversity (36 forms) and dominance of 1–2 species suggesting environments of either an estuary, or a coastal bay. (2) The *Chatangiella tripartite* assemblage: considerably abundant *Hystrichosphaeridium tubiferum* (Ehr.) Defl., *Membranilarnacia angustivela* (Defl. et Cook.) McMinn, *Spiniferites ramosus ramosus* Ehr., *Spongodinium delitiense* (Ehr.) Defl., *Cerodinium striatum* (Drugg) Lent. et Will., *Chatangiella tripartita*, and *Trithyrodinium robustum*; a high diversity of dinocysts (82 species); environments of internal to external shelf. (3) The *Palaeocystodinium australinum* assemblage: dominant *Kleithriasphaeridium truncatum* (Ben.) Stov. et Evitt, *Cribroperidinium wetzelii* (Lej.-Carp.) Hel., *Palaeocystodinium australinum* (Cook.) Lent. et Will., and *Pierceites pentagonus* (May) Hab. et Drugg; comparatively high diversity of dinocysts (55 species); normal marine environments of a coastal bay. (4) The *Areoligera* sp.–*Exochosphaeridium bifidum* assemblage: highly abundant *Areoligera* sp., *Exochosphaeridium bifidum* (Clarke et Verd.) Clarke et al., *Cleistosphaeridium placacanthum* (Defl. et Cook.) Eat. et al., *Chatangiella tripartita*, and *Trithyrodinium striatum* Ben.; comparatively high diversity of dinocysts (53 species); dominant in the assemblage are *Areoligera* and *Exochosphaeridium bifidum*; nearly normal marine environments of a coastal bay.

A comprehensive analysis of the upper Cenomanian–upper Coniacian deposits in southern England clearly showed dependence of dinocysts on particular geochemical parameters, i.e., the different ecological adaptation of these microorganisms to habitat environments (Pearce et al., 2003). According to results of cluster analysis and correlation with geochemical data, the studied dinocysts were divided into three species groups characterizing different geochemical conditions.

Two different assemblages of dinocysts have been also distinguished in the Turonian–Coniacian deposits of the North Sea, England and France (Pearce et al., 2003). The "*Spiniferites–Palaeohystrichophora*" (S–P)

assemblage of a high taxonomic diversity includes abundant gonyaulacoid (*Spiniferites, Achomosphaera, Pterodinium*) and peridinioid cysts (primarily *Palaeohystrichophora infusorioides* in the Anglo–Parisian basin but *Chatangiella, Isabelidinium*, and *Trithyrodinium* in the North Sea). The "*Circulodinium–Heterosphaeridium*" (C–H) assemblage is dominated by gonyaulacoid cysts (*Circulodinium, Heterosphaeridium*) characteristic of coastal water masses. The C–H assemblage is typical of northwestern marginal zone of the Anglo-Parisian basin, whereas the diverse S–P assemblage is confined to deeper central areas of the basin (Pearce et al., 2003).

Li and Habib (1996) considered the *Spiniferites/Cyclonephelium* ratio as indicative of sedimentation environments. They regarded the *Spiniferites* group as typical of environments of an open sea shelf and the *Cyclonephelium* group as characteristic of coastal or comparatively isolated settings. In opinion of cited researchers, the S/C index is more sensitive indicator of environmental changes than the species diversity and increases away from the shoreline (Li and Habib, 1996).

Acritarchs. As is argued in many works, acritarchs are commonly confined to shallow-shelf deposits and can be used to establish the initial and terminal stages of transgressions (Downie et al., 1971). Small acanthomorphic acritarchs occur in a wide spectrum of marine environments. Acritarchs, prasinophytes and dinoflagellates are known from the Maastrichtian black mud deposited in the Atlantic Ocean under the high-productive conditions of upwelling (Firth and Clark, 1998). Nevertheless, small acritarchs of the *Michrystridium* group are most common in coastal sandy deposits. In many cases, acritarchs are concentrated in coarse-grained sediments in contrast to other palynomorphs prevailing in fine-grained deposits. Wall (1965) argued for confinement of *Michrystridium* having long processes to Jurassic deposits of calm sedimentation settings in contrast to species with reduced processes occurring in sandstones characterizing a more active hydrodynamics. Fechner (1996) discovered the diverse assemblages of small acritarchs in littoral sandstones and of large dinocysts in overlying clays (the Oligocene of Germany). Small acritarchs described in work by Schrank (2003) have been macerated from the Campanian–Maastrichtian sediments deposited on a flat shelf. Small acritarchs dominate here in the phosphatic formation of relatively coarse-grained bioturbated sediments deposited at the initial phase of sea transgression. The other palynomorphs, mostly spores and pollen of terrestrial plants (10–20 μm) and dinocysts of the genus *Dinogymnium*, are extremely rare in this formation, whereas large dinoflagellates are dominant in a layer 10 cm thick, enclosed into the phosphatic sandstones.

Harris and Tocher (2003) who studied different Cenomanian–Turonian facies of the West Interior basin

of North America established confinement of *Eyrea nebulosa* Cook. et Eis., *Leiofusa jurassica* Cook. et Eis., and *Micrhystridium recurvatum* Val. to shallow-water settings with lowered salinity of seawater. Some species, for instance *Micrhystridium stellatum* Defl. and *Scuticabolus lapidaries* (O. Wetz.) Loeb. III were presumably of stenohaline type, whereas habitats of *Tetraporina* and *Wuroia* forms were constrained by deep waters (Harris and Tocher, 2003).

Prasinophytes. This group of green algae is para-doxical, because their mass abundance is typical of deep-water oxygen-deficient environments, on the one hand, and of coastal, well freshened waters, on the other. Richardson (1984) established confinement of genera *Leiosphaeridia* and *Tasmanites* to the Silurian and Devonian deep-water shales and was of opinion that these taxa are comparable in morphology with recent genera *Halosphaeridia* and *Pachysphaera*, the pelagic algae, which can submerge down to the depth over 2000 m and then return quickly into the upper water layer.

Il'ina (1985) analyzed distribution of microphyto-plankton in the Jurassic–Lower Cretaceous sediments of the Nordvik Peninsula (Khatanga region), which are of comparatively deep-water genesis, and distinguished two types of assemblages alternating in the section. One assemblage consisting of dinocysts associated with subordinate acritarchs and prasino-phytes is confined to sediments deposited at a sufficient depth under conditions of well-aerated bottom waters. The other assemblage of scarce dinocysts mostly repre-sented by *Leiosphaeridia* and *Pterospermella* species is typical of sediments accumulated in deep anoxic waters probably polluted by hydrogen sulfide.

Prauss and Riegel (1989) discussed in their work a problem concerning the current ecology of prasino-phytes and their confinement to sedimentary facies. Based on integrated data of paleogeographic and cli-matic analysis, stable isotopes distribution in deposits containing prasinophytes (the lower Toarcian *Posi-donia* Shales of Europe) and current habitat environ-ments of these organisms, they established that bloom of prasinophytes is characteristic of cold sea waters with a considerably lowered salinity. As a result, they concluded that black shales enriched in prasinophytes originated by the salinity-controlled water layering. On the other hand, black shales with phytoplankton assem-blages, in which prasinophytes are allied with dinocysts and acritarchs, could be formed below thermocline or in upwelling zone but not because of the halocline development (Prauss and Riegel, 1989). Specific requirements to nutrition could likely be superposed on these factors.

***Paralecaniella* group.** This genus initially attrib-uted to Volvocophyceae and then to dinocysts (Elsik, 1977) is now regarded as a group of unclear systematic position (Fensome et al., 1990). Palynological analysis of the Maastrichtian deposits in the Netherlands

showed that assemblages of palynomorphs are domi-nated either by dinocysts, or by *Paralecaniella* species (Schiöler et al., 1997). As is assumed, abundance of the latter characterizes a proximal coastal zone with a high hydrodynamic activity and possible stress conditions (Brinkhuis and Schiöler, 1996), whereas the diversity of dinocyst assemblages points to sedimentation in ner-itic settings and tranquil hydrodynamics. The alterna-tion of different assemblages in the section was con-nected in the cited work with the relative sea-level changes. In the Cretaceous–Paleogene deposits of the Netherlands, Herngreen et al. (1998) also distinguished two types of assemblages: (1) the relatively impover-ished assemblage dominated by *Paralecaniella* and (2) the diverse assemblage with prevalent dinocysts. Data on distribution of *Paralecaniella* forms in Upper Creta-ceous deposits of the Ust-Yenisei region show that they are distinctly confined to leptochlorite sands. Dinocysts are of a very low taxonomic diversity or even absent in phytoplankton assemblages dominated by this genus (Lebedeva and Zverev, 2003).

FACIES-DEPENDENT DISTRIBUTION OF PALYNOMORPHS IN UPPER CRETACEOUS DEPOSITS OF THE UST-YENISEI REGION

A thorough lithological and paleontological study of Upper Cretaceous deposits in the Ust-Yenisei region provided an opportunity to trace the facies changes and to plot the transgressive-regressive variation curve characterizing the integrated section shown in Fig. 1 (Zakharov et al., 1991, 2003; Sahagian et al., 1996).

Assemblages of microphytofossils, which succes-sively replace one another in the section, can be regarded as facies-dependent. An assemblage is regarded in this work as a complex of palynological spectra, separate palynomorph groups of which occur in slightly changeable, almost persistent proportions. The distinguished types of assemblages characterize the progressively growing offshore distance of respec-tive phytoplankton communities (from continental to relatively deep-water habitats) and have been used along with sedimentological data to plot the curve of sea-level fluctuations recorded in the Ust-Yenisei sec-tion (Fig. 1).

Let us consider characterization of each assem-blage.

(1) Rocks: cross-bedded sands with coalified wood, amber, and interlayers of coalified plant detritus, clayey aleurite and occasional clay.

Characterization of the assemblage: predominantly spores and pollen (90–100%), spores of aquatic ferns are rather frequent. Microphytofossils are represented by freshwater genera *Schizosporis, Schizocystia*, and *Tetraporina*.

(2a) Rocks: sands, sands with clay laminae and aleurites, frequently bioturbated, containing rare cal-careous and phosphatic concretions.

Characterization of the assemblage: spores and pollen are dominant. Abundance rates of phytoplankton groups: 0–10% of freshwater algae, 0–8% of acritarchs (*Micrhystridium, Veryhachium, Leiofusa*), 0–12% of prasinophytes (*Pterospermella, Cymatiosphaera*), 5–45% of *Paralecaniella* forms. The gonyaulacoid group is dominant among dinocysts. Chorate cysts (*Pervosphaeridium, Spiniferites, Oligosphaeridium, Exochosphaeridium, Downiesphaeridium*) representing 0–40% occur in association with abundant and diverse cavate forms (*Chatangiella, Trithyrodinium, Alterbidinium, Palaeohystrichophora infusorioides*). Holocavate *Chlamydophorella* and *Chlonoviella* may occur as subordinate components (up to 6%). Presence of proximochorate cysts of the *Cyclonephelium–Circulodinium* group, *Fromea* and *Microdinium* (sometimes over 5%) is also characteristic.

(2b) Rocks: sands with rare clay laminae and minor amount of leptochlorite frequently contain siderite concretions.

Characterization of the assemblage: spores and pollen are dominant, associated with extremely impoverished assemblage of marine palynomorphs. Abundance of all the groups is insignificant except for freshwater algae (5–20%) and *Paralecaniella* species (up to 50%). Dinocysts are of extremely low diversity. The most essential components are *Fromea* and subordinate cysts of the *Cyclonephelium–Circulodinium* group, *Chatangiella, Spiniferites*, and *Oligosphaeridium*.

(3) Rocks: leptochlorite sands with numerous phosphatic, calcareous and sandy concretions containing diverse fauna.

Characterization of the assemblage: *Paralecaneilla* forms are dominant (80–100%). Dinocysts either absent, or their composition is very simple. Characteristic is absence of chorate cysts, the representatives of *Pterospermella* and *Schizosporis* groups.

(4) Rocks: sands with clay laminae sometimes, containing calcareous and less frequent phosphatic concretions, aleurites, and members of interlayering sand, aleurite and clayey aleurite.

Characterization of the assemblage: spores and pollen dominate; freshwater algae represent 0–10%, acritarchs 0–20%, prasinophytes 0–12%, and *Paralecaneilla* 0–20%. The peridinioid group dominant among dinocysts largely consists of cavate forms (*Chatangiella, Trithyrodinium, Alterbidinium, Palaeohystrichophora infusorioides*). *Microdinium, Rhiptocorys*, and *Glyphanodinium* can be numerous among proximate cysts. Chorate cysts of a very uniform composition represent 0–24%.

(5) Rocks: aleurites, clayey and sandy aleurites, the latter sometimes containing calcareous and less frequent phosphatic concretions.

Characterization of the assemblage: spores and pollen dominate; freshwater algae represent 0–5%, acritarchs 0–15%, prasinophytes 1–25%, and *Paralecaneilla* forms 0–40%. The peridinioid cysts dominate in the dinocyst group. The diverse cavate and proximate cysts are approximately equal in abundance, while chorate and holocavate forms are rare.

(6) Rocks: clays and silty clays with calcareous concretions.

Characterization of the assemblage: prevalence of marine microphytoplankton. Freshwater algae, acritarchs, prasinophytes, and *Paralecaneilla* occur sometimes as subordinate components. The dinocyst group is dominated by either gonyaulacoid, or peridinioid cysts with respective alternation of dominants. Abundance rates of diverse cavate and proximate cysts are approximately equal. Chorate cysts represent up to 40%.

(7) Rocks: clays and silty clays.

Characterization of the assemblage: marine microphytoplankton dominates. Freshwater algae and acritarchs are absent. Percentages of prasinophytes and *Paralecaneilla* forms are low. Peridinioid cavate cysts dominate in the dinocyst group that includes all the morphotypes, thus being very diverse.

The analyzed distribution of palynomorph assemblages, their correlation with the facies variation trend and available lithological and paleontological data facilitated division of above assemblages into four biofacies. These are the continental (assemblage 1), coastal-marine (assemblages 2a, 2b, 3), shallow-water (assemblages 4 and 5), and deep-water (assemblages 6 and 7) biofacies characterizing the extent of microphytoplankton remoteness from shoreline.

The terms "shallow-water" and "deep-water" are certainly conditional, because microphytoplankton cannot be actually indicative of the basin depth. In fact, the terms mean its remoteness from shoreline, as this factor controls proportions between terrestrial and marine taxa or the content of freshwater algae, acritarchs, prasinophytes, and different dinocyst morphotypes.

The distinguished assemblages, trends in distribution of different microphytofossils groups, and ecologic data represent basis for biofacies analysis of the Upper Cretaceous deposits in the Ust-Yenisei region.

At the base of the Upper Cretaceous succession, there is a sequence of continental alluvial-deltaic sands of the Dolgan Formation, which are exposed along the Nizhnyaya Agapa River. Observable above is a gradual transition from continental to deep-shelf facies (Fig. 1). The shallow-water marine deposits contain diverse assemblages of fossil invertebrates and dinoflagellate cysts. The respective transgression progressed quickly deepening the basin. The subsequent fast regression was responsible for accumulation of the higher member composed of sands and aleurites, which are barren of macrofossils and contain only palynomorphs of marine and continental genesis. The respective lithofacies and structure of palynomorph assemblages have been described in detail by Lebedeva and Zverev (2003).

The middle Turonian sedimentary succession exposed at the Chaika River begins with continental cross-bedded sands containing predominantly the freshwater microfossils (Fig. 2). The subsequent sedimentation progressed in a coastal zone and shallow shelf settings with active hydrodynamics, quickly changing environments and local freshening. The lower Member I corresponding to deposits of a brackish-water bay (Zverev, 1999) contains the dinocyst assemblage of a very low diversity. Its dominant taxa are *Circulodinium distinctum, Trithyrodinium suspectum*, sometimes *Fromea*. Gonyaulacoid cysts prevail over peridinioid ones. Chorate cysts are rare, but in some clay interlayers their content corresponds to 20–30% (*Pervosphaeridium, Spiniferites*). Macrofauna is absent. In Member II representing deposits of a small mouth bar and pre-frontal beach zone (Zverev, 1999), dominant groups include *Chatangiella* and *Chlonoviella* in addition. Characteristic of the overlying shelf complex (Zverev, 1999) is prevalence of peridinioid cysts over gonyaulacoid forms and presence of *Pterospermella* and *Cymatiosphaera*. The dominant taxon is *Trithyrodinium suspectum*. Coastal-marine sediments contain a diverse inoceramid assemblage. The frequent change of assemblages, mostly of assemblages 2 and 3, is a characteristic feature of the Chaika River section. Dinocysts of a low taxonomic diversity are not abundant that is probably a result of periodical salinity decline and active hydrodynamics. Peridinioid cavate cysts (*Trithyrodinium, Chatangiella*) represent the group most tolerant to environmental changes. Leptochlorite sands contain the monodominant **assemblage 3** with *Paralecaniella* and *Leiosphaeridia*. A sharply reduced abundance of spores and pollen is recorded at the same level, as they probably have disappeared under influence of active hydrodynamics.

The upper Turonian–upper Coniacian deposits of the Yangoda River section also characterize variable environments of sedimentation. Practically complete succession from coastal to shelf facies is recognizable here in the section lower part, exemplifying here the transgressive trend of sedimentation. Dinocysts of a very low abundance and diversity, dominated by *Trithyrodinium suspectum*, are characteristic of the lower Member I. In Member II, amount of their taxa is greater, and *Chatangiella* and *Microdinium* are dominant. Two monodominant **assemblages 3** with *Paralecaniella* are distinguished, and prevalence of peridinioid, mostly cavate cysts is established. Chorate cysts practically disappear parallel to growing abundance of prasinophytes and acritarchs and to declining content of *Paralecaniella* forms and freshwater algae. The dominant dinocyst taxon is *Chatangiella*. The transgression peak corresponds to jarosite clays at the Turonian–Coniacian boundary (Member VIII). The most diverse dinocysts appear somewhat higher (Member IX, **assemblage 6**). Effects of local freshening are recorded in members XI–XIV, where abundance and diversity of dinocysts is considerably reduced, and only

Fromea morphotypes are sufficiently abundant. Acritarchs and prasinophytes are rare, whereas content of *Paralecaniella*, freshwater algae, and spores of aquatic ferns is growing. Numerous siderite concretions occurring in deposits point to relatively shallow-water sedimentation settings. Fauna disappears in the upper part. The higher members XVI–XX are again enriched in marine microphytoplankton. Gonyaulacoid, primarily chorate forms (*Oligosphaeridium, Spiniferites*) prevail among dinocysts. Acritarchs and prasinophytes are either rare or absent. In the upper Coniacian (members XXII-XXV), gonyaulacoid cysts either prevail over peridinioid forms, or are comparable in abundance with the latter. *Paralecaniella* and acritarchs occur as subordinate components.

Near the settlement Vorontsovo, the Upper Coniacian deposits belong to facies of a shallow shelf and characterize a general transgressive trend recorded in the section from the base upward (Fig. 4). In the section lower part (members I and II), alternating **assemblages 2a** and **3** suggest unstable character of sedimentation in shallow-water settings with active hydrodynamics. Dinocysts are not diverse, and only *Trithyrodinium suspectum, Chlamydophorella nyei*, and *Fromea* are sufficiently widespread. Higher in the section (**assemblages 4** and **6**) there is established presence of all the dinocyst morphogroups, slight fluctuations in their abundance, and absence of freshwater microfossils. These features are indicative of normal salinity and rather uniform habitat environments. Gonyaulacoid, mostly chorate cysts (*Pervosphaeridium, Spiniferites*) prevail in **assemblage 6.**

In the Tanama River section, basal monotonous aleurites of continental origin are barren of macro- or microfauna and dinocysts. These sediments containing only spores and pollen of terrestrial plants and freshwater algae are overlain by transgressive succession of sands and aleurites. Abundant marine fauna occurring in the Santonian deposits is an evidence of normal marine regime in the basin (Zakharov et al., 1991). Abundance rates of different palynomorph groups are rather stable throughout the interval of marine sediments (Fig. 5). **Assemblage 4** characteristic of the lower and upper parts (members 1 and III) is dominated by peridinioid cysts of genera *Trithyrodinium, Chatangiella*, and *Alterbidinium*. The content of chorate cysts (*Fibrocysta, Oligosphaeridium, Spiniferites*) in aleurite beds is up to 36%. The *Paralecaniella* group, *Pterospermella* group, and holocavate cysts occur as minor components. The content of freshwater algae is up to 10% (especially in the section lower part). In Member II and at the base of member III, there are recorded sharp variations in abundance of peridinioid and gonyaulacoid cysts, since the decreasing content of *Chatangiella* is accompanied by growing proportion of *Fromea* and *Microdinium*. Microphytofossils are comparable here in composition with **assemblage 2a,** but the *Cyclonephelium* group is missing.
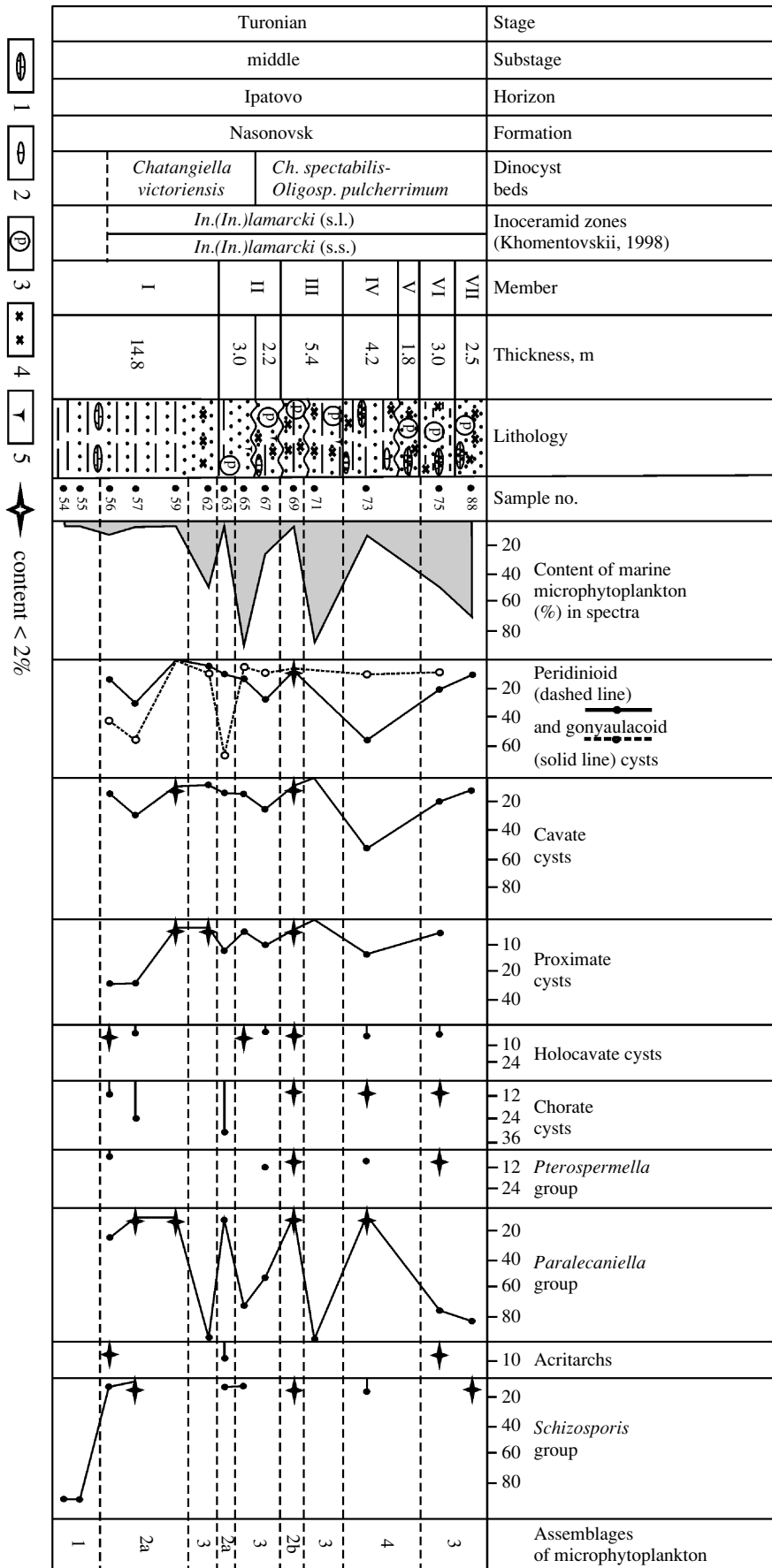
Fig. 2. Palynological diagram for the Chaika River section: (1) calcareous, (2) siderite and (3) phosphatic concretions; (4) leptochlorite; (5) bioturbation (other symbols as in Fig. 1).
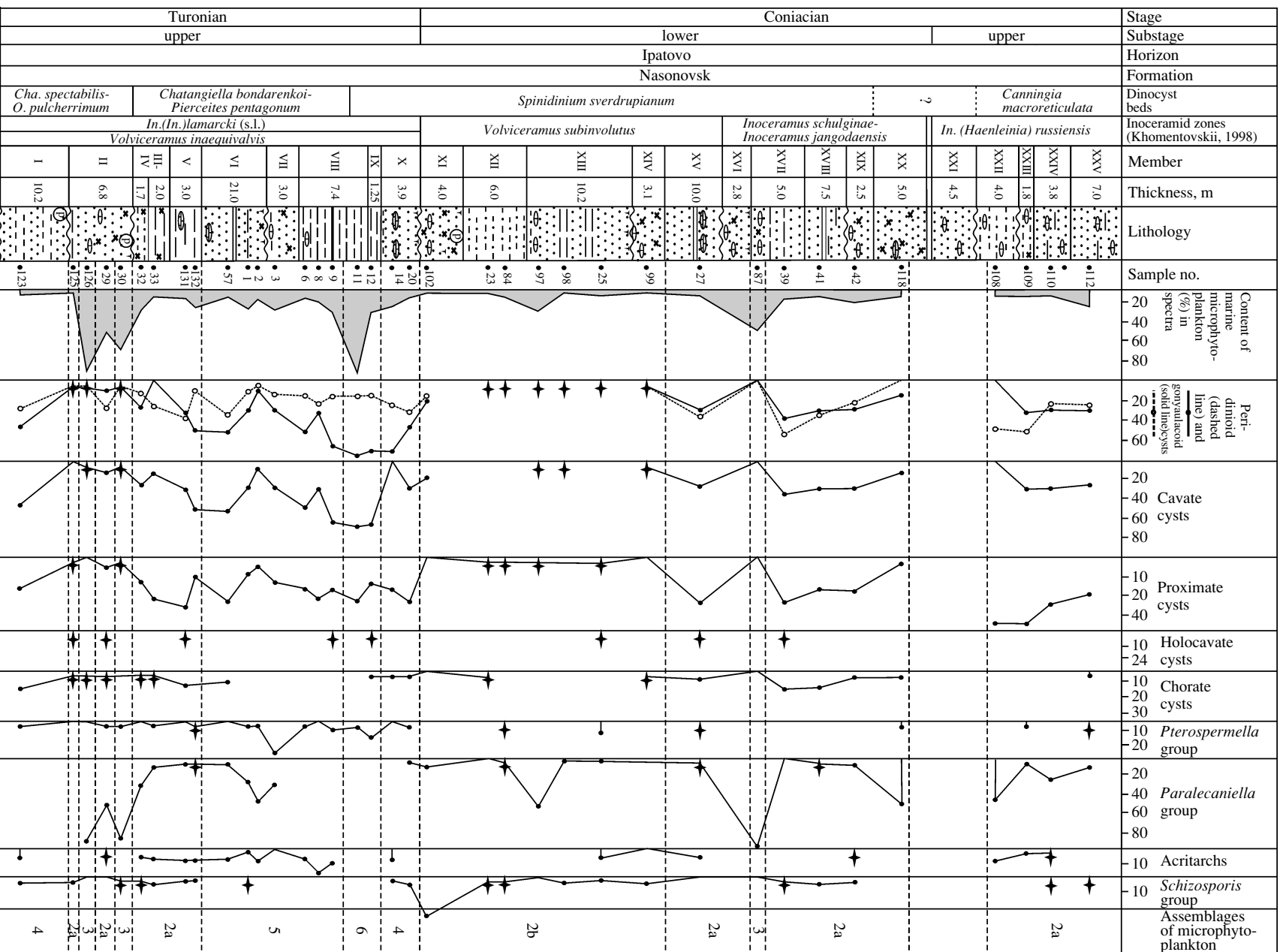
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Fig. 3. Palynological diagram for the Yangoda River section (other symbols as in Figs. 1 and 2).

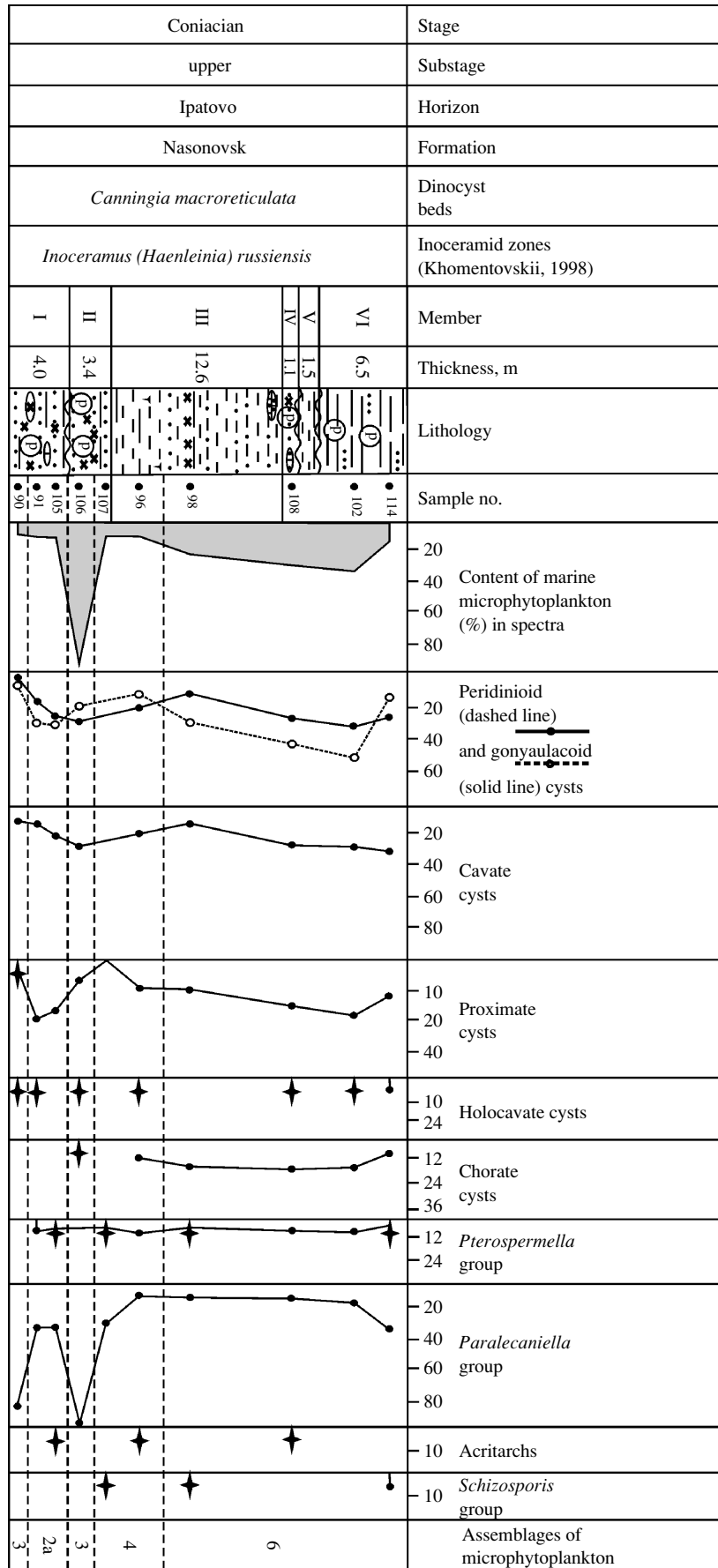|	
Coniacian	Stage
upper	Substage
Ipatovo	Horizon
Nasonovsk	Formation
Canningia macroreticulata	Dinocyst beds
Inoceramus (Haenleinia) russiensis	Inoceramid zones (Khomentovskii, 1998)
I II III IV V VI	Member
4.0 3.4 12.6 1.1 1.5 6.5	Thickness, m
	Lithology
90 · 91 · 105 · 106 · 107 · 96 · 98 · 108 · 102 · 114	Sample no.
20 / 40 / 60 / 80	Content of marine microphytoplankton (%) in spectra
20 / 40 / 60	Peridinioid (dashed line) and gonyaulacoid (solid line) cysts
20 / 40 / 60 / 80	Cavate cysts
10 / 20 / 40	Proximate cysts
10 / 24	Holocavate cysts
12 / 24 / 36	Chorate cysts
12 / 24	*Pterospermella* group
20 / 40 / 60 / 80	*Paralecaniella* group
10	Acritarchs
10	*Schizosporis* group
3 2a 3 4 6	Assemblages of microphytoplankton

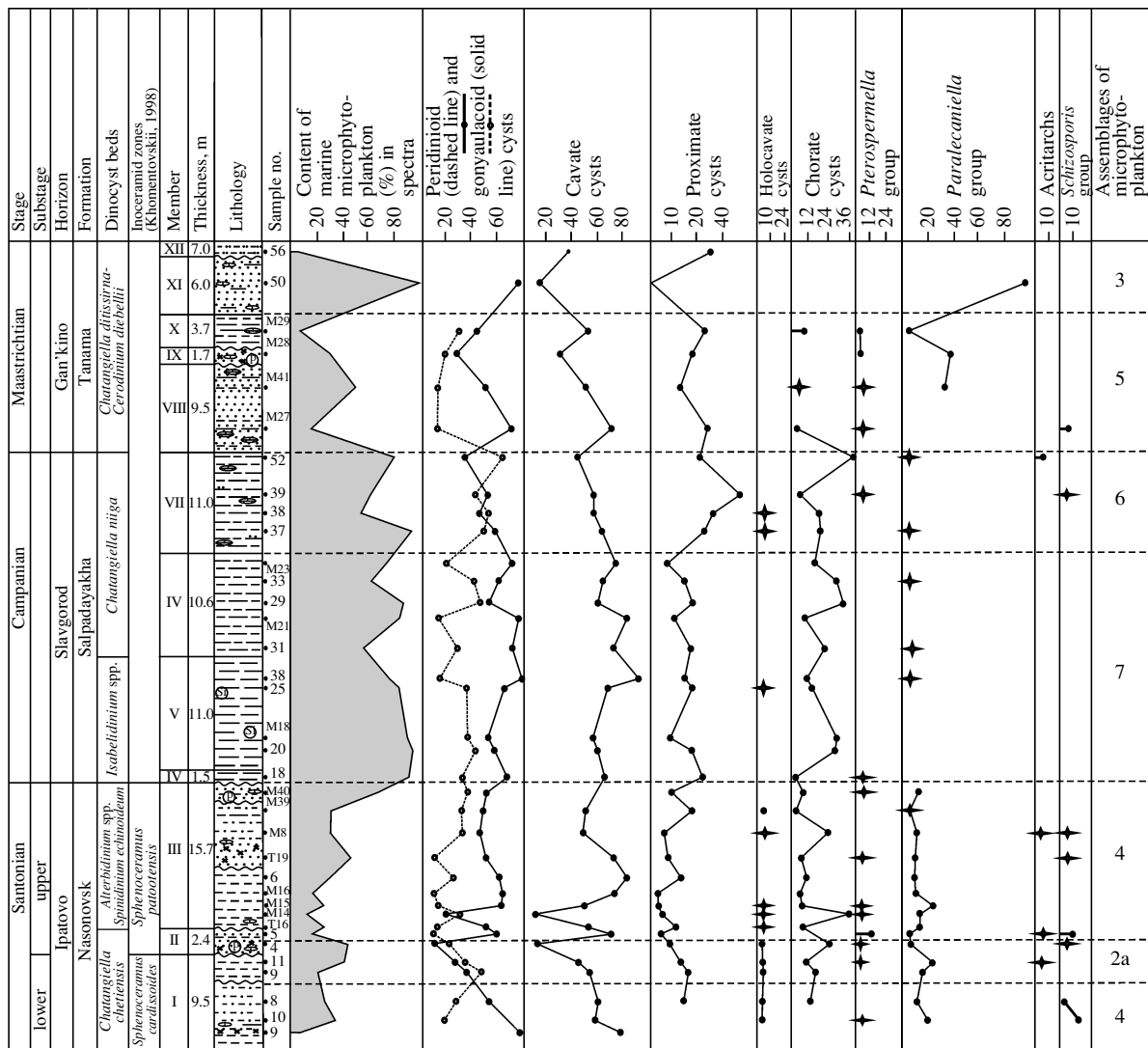**Fig. 4.** Palynological diagram for the Vorontsovo section (other symbols as in Figs. 1 and 2).

Fig. 5. Palynological diagram for the Tanama River section (other symbols as in Figs. 1 and 2).

The deeply eroded surface of Santonian deposits is overlain by the Campanian opoka-like clays. Inoceramids and other groups of marine fauna, which are abundant in Santonian sediments do not occur above the latter. Composition and proportions of palynomorphs change sharply as well (Fig. 5). Dinocysts dominate in members IV and V (80–100%). Peridinioid cysts (*Trithyrodinium, Chatangiella, Isabelidinium, Alterbidinium*) prevail over the others. Chorate cysts (*Fibrocysta, Oligosphaeridium, Spiniferites, Prolixosphaeridium*) are sufficiently abundant (up to 30%) but not diverse. Representatives of the genus *Laciniadinium* dominate in the group of proximate cysts; percentage of *Fromea* is perceptible (especially in Member IV). The other persistent but not abundant components are *Odontochitina, Cyclonephelium/Circulodinium* group, *Microdinium*, and *Palaeohystrichophora infusorioides*.

The Campanian–Maastrichtian interval of the Tanama section clearly corresponds to the regressive sedimentary succession (Zakharov et al., 1991). Concentration of terrestrial spores and pollen is increased in Member VII (**assemblage 6**), where freshwater algae appear in addition. Peridinioid and gonyaulacoid forms alternately dominate among dinocysts. Cavate and proximate cysts occur in approximately equal proportions. Spores and pollen of terrestrial plants dominate in **assemblage 5** confined to members VIII–X of the Maastrichtian interval. Characteristic of this assemblage are the following features: prevalence of peridinioid over gonyaulacoid forms, approximately equal proportions of cavate and proximate cysts, occurrence of single chorate cysts, and appearance of *Paralecaniella* (up to 40%). The *Paralecaniella* dominance is established in Member XI (**assemblage 3**). The described succession is overlain by the Danian continental sands.

CONCLUSION

The review of works dedicated to ecology of present-day and fossil dinoflagellates and their cysts showed that available data are insufficiently adequate for comprehensive facies reconstructions. Consequently, it is necessary to study further how different environmental factors controlled distribution of fossil dinocysts and other palynomorphs in the sections well studied by paleontological and sedimentological methods. One of such reference sections is the Upper Cretaceous sedimentary succession of the Ust-Yenisei region, which is a perfect object for establishing the facies trends in distribution of dinocysts and other representatives of microphytoplankton.

In this work, different groups of palynomorphs (spores and pollen of terrestrial plants, dinoflagellate cysts, prasinophytes, acritarchs, zygnematacean algae, and other taxa of unclear taxonomic affinity) have been studied in different facies of Upper Cretaceous deposits. The main objective was to reveal impacts of local and global environmental factors on their distribution trends and to understand paleoecology of separate microphytoplankton groups.

Seven assemblages of palynomorphs have been distinguished based on quantitative proportions of terrestrial and marine components, percentages of separate morphological groupings, and taxonomic composition of microphytoplankton. According to composition and ecologic peculiarities of dominant groups, geological and sedimentological data, the distinguished assemblages are attributed to four facies of continental, coastal-marine, shallow- and deep-water types.

The comparative analysis of the Upper Cretaceous stratigraphic subdivisions, dinocyst and other palynological biofacies showed that boundaries of biostratigraphic units not always coincide with levels of lithofacies changes. This evidence a weak facies dependence of dinocysts at least in the West Siberian epicontinental basis that has been studied. Consequently, dinocysts are proved to be of a high stratigraphic significance and correlation potential. As is established besides, trends in distribution of dinocysts and other palynomorphs are correlative with transgressive-regressive cycles and can be used by reconstruction of paleoenvironments.

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